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# **THE ECO-PHYSIOLOGY OF TWO CONTRASTING ARID-ZONE WOODLANDS IN AUSTRALIA**

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**Doctor of Philosophy – Science  
PhD by Research**

**2019  
UNIVERSITY OF TECHNOLOGY SYDNEY**

## ***Certificate of Original Authorship***

I certify that the work in this thesis has not previously been submitted for a degree nor has it been submitted as part of requirements for a degree except as fully acknowledged within the text.

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## *In memory of*

*Baltazar Terrazas Valdes (1956-2015), who had an incredible appreciation and passion for the natural world, and words cannot express how special he was for me.*

*Karla Nathaly Leon Velazquez (1987-2015), who was and will always be the best team I've ever had.*

*Jade Terrazas Bajo (2007-2018), I would much prefer it if you were alive and well.*

## *Acknowledgements*

I would like to acknowledge the support of the University Technology of Sydney (UTS) and the Consejo Nacional de Ciencia y Tecnología for the graduate fellowship (232184). This work was supported by an Australian Research Council grant awarded to Derek Eamus (DP14101150). A portion of the material present in this thesis is based upon work supported in part by OzFlux within the Terrestrial Ecology Research Network (TERN) and the Terrestrial Eco-hydrological Research Group at UTS.

I have been doubly privileged to call the stunning Sonoran Desert home and to complete a PhD on eco-physiology studying the spectacular semi-arid region in central Australia. For encouraging my interest on eco-hydrological studies and embracing my early career as a scientist, for all your support, guidance and endless advice, I will always be grateful to Dr. Jaime Garatuza-Payán and Dr. Enrico A. Yépez from The Sonoran Institute of Technology.

For all the exceptional guidance and support to make this thesis possible, I am extremely thankful for my supervisor Professor Derek Eamus who took the time to read many drafts of this thesis. Thanks Derek, for your patience and the many questions that helped to improve my reasoning in eco-physiology. I would like to thank my co-supervisor Dr. Rachael Nolan for her quality advice and dedication since the beginning of my PhD study. To Dr. James Cleverly, thanks for his insightful comments and for helping me to comprehend OzFlux data and many eco-physiological processes. I am also thankful to Professor Belinda Medlyn for supporting my research in central Australia and providing supervision through this thesis. I appreciated from all of you, your helpful suggestions, reviews and comments to improve my PhD thesis.

This thesis would also not have been accomplished without my family support. To my parents and sisters who were always there for me in the most difficult situations despite the distance between us. I am deeply grateful to all my family back in Mexico for the endless calls and the many motivational words that were a source of solace during the time I spent in Australia.

I would like to give a special thanks to Sheilla B. Syd Julian, Layla J.B., Deeni C. and Ivan C. who were my piece of México in a foreign country.

To my fellows at UTS, I thank you for sharing all your amazing stories, for all the good times and for making this journey the most enjoyable adventure. To my friends back in Mexico and across the world: Ann-Marie Rohlf, Rachel Gray, Zulia Sánchez, Corina Quiroz, Asis Hallab, Fernando Castillo, Sammuell Villarreal, Laura Celis, An Tran, Marco Giardina, John Gallego, Rizwana Rummani, Carlos Ibarra, Sam Goyen, Rendy Ruvindy, Lorenzo Barolo, Marihta Harahap, Bojana Manojlovic, Alex Thomson, Qiaoyun Xie, Sofie Voerman, Kirsty Milner, Marco Alvarez, Paloma Matis, Divia Vinod, Tiziana Zingali, Eva Fernandez, Lia Barresi, Andrew Olivera, Oriana Cresta, Ewen Beard and Alistar Walsh. I greatly appreciated the innumerable supportive and motivating words you gave during my PhD studies and beyond.

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## Abbreviations, acronyms and symbols

$A$	Carbon assimilation	$(\mu\text{mol m}^{-2} \text{ s}^{-1})$
AIC	Akaike information criterion	
$A_{\text{max}}$	Maximum gross photosynthetic rates	$(\mu\text{mol m}^{-2} \text{ s}^{-1})$
$A_n$	Net photosynthetic carbon uptake	$(\mu\text{mol m}^{-2} \text{ s}^{-1})$
$A_{n2000}$	Net photosynthetic carbon uptake at PPFD= 2000 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$	$(\mu\text{mol m}^{-2} \text{ s}^{-1})$
ANN	Artificial neural network	
ANOVA	Analysis of variance	
BoM	Bureau of Meteorology	
C	Carbon	
$C_a$	Atmospheric $\text{CO}_2$ concentration	$(\mu\text{mol mol}^{-1})$
CFI	Comparative fit index	
$C_i$	$\text{CO}_2$ concentration inside leaf air spaces	$(\mu\text{mol mol}^{-1})$
CUE	Carbon-use-efficiency	(daily C gain <i>per</i> mol C fixed)
C3	Carbon fixation pathway where $\text{CO}_2$ is fixed by Rubisco	
C4	Carbon fixation pathway where $\text{CO}_2$ is fixed by PEP-Carboxylase	
$\text{CO}_2$	Carbon dioxide	
$E$	transpiration	$(\text{mol m}^{-2} \text{ s}^{-1})$
EC	Eddy covariance	
ENSO	El Niño-Southern Oscillation	
ER	Ecosystem respiration	$(\text{gC m}^{-2} \text{ d}^{-1})$
ET	Evapotranspiration	(mm)
$\text{ET}_0$	Reference ET	(mm)
EVI	Enhanced vegetation index	
D	Vapour pressure deficit at the leaf surface	(kPa)
D2, D3	Second and third drought, respectively	
DCG	Daily carbon gain	$(\text{mol C m}^{-2} \text{ d}^{-1})$
G	Ground heat flux	$(\text{W m}^{-2})$
$G_c$	Canopy conductance	$(\text{mmol m}^{-2} \text{ s}^{-1})$
GLSA	Global land sink anomaly	
GPP	Gross primary production	$(\text{gC m}^{-2} \text{ d}^{-1} \text{ or } \mu\text{mol mol}^{-1})$
$g_0$	Conductance when photosynthesis is zero	$(\text{mol m}^{-2} \text{ s}^{-1})$
$g_1$	Optimal stomatal model inversely related to $\text{WUE}_i$	$(\text{kPa}^{0.5})$
$g_s$	Stomatal conductance	$(\text{mol m}^{-2} \text{ s}^{-1})$
$g_c$	Stomatal conductance for $\text{CO}_2$	$(\text{mol m}^{-2} \text{ s}^{-1})$
H	Sensible heat flux	$(\text{W m}^{-2})$
$\text{H}_2\text{O}$	Water vapour	
IRGA	Infrared gas analyzer	
LAI	Leaf area index	
LCP	Light compensation point	$(\mu\text{mol photon m}^{-2} \text{ s}^{-1})$
LE	Latent heat flux	$(\text{W m}^{-2})$
LMA	Leaf mass <i>per</i> area	$(\text{g m}^{-2})$
LRC	Light response curve	
LSP	Light saturation point	$(\mu\text{mol photon m}^{-2} \text{ s}^{-1})$
LUE	Light-use-efficiency	$(\text{mmol CO}_2 \mu\text{mol}^{-1} \text{ photon})$
MAP	Mean annual precipitation	
MODIS	Moderate resolution imaging spectroradiometer	
N, $\text{N}_2$	Nitrogen	
$N_a$	Foliar N concentration <i>per</i> leaf area	$(\text{g N cm}^{-2})$
NEE	Net ecosystem exchange	$(\text{gC m}^{-2} \text{ d}^{-1})$

NEP	Net ecosystem production	(gC m <sup>-2</sup> d <sup>-1</sup> )
P	Precipitation	(mm)
PAR	Photosynthetically active radiation	(μmol mol <sup>-1</sup> )
PDB	Pee Dee Belemnite	
PET	Monthly Penman-Monteith reference ET	
PFT	Plant functional type	
$P_{gross}$	Gross photosynthesis	(mol C m <sup>-2</sup> d <sup>-1</sup> )
$P_{net}$	Net photosynthesis during the day	(mol C m <sup>-2</sup> d <sup>-1</sup> )
PM	Penman-Monteith	
PNUE	Photosynthetic nitrogen-use-efficiency	((μmol CO <sub>2</sub> ) <i>per</i> (g N) <sup>-1</sup> s <sup>-1</sup> )
PPFD	Photosynthetic photon flux density	(μmol mol <sup>-1</sup> )
PPT	Rainfall	(mm)
QA/QC	Quality assurance/control	
R	Project software® for language statistical computing and graphics	
$r_a$	Aerodynamic resistance	(s m <sup>-1</sup> )
$R_d$	Dark respiration also $R_{dark}$	(μmol m <sup>-2</sup> s <sup>-1</sup> )
$R_{het}$	Heterotrophic respiration	
$r_L$	Leaf resistance	(s m <sup>-1</sup> )
$R_n$	Net radiation	(W m <sup>-2</sup> )
$R_{night}$	Nocturnal respiration	
$R_{plant}$	Plant respiration	(μmol m <sup>-2</sup> s <sup>-1</sup> )
$R_{sample}$	Ratio of heavy to light isotopes in a sample	
$R_{standard}$	Ratio of heavy to light isotopes in a standard	
RUE	Resource-use-efficiency	
SE	Standard error	
SEM	Structural equation modelling	
SPEI	Standardized precipitation-evapotranspiration drought index	
SOFM	Self-organizing feature map	
SOLO	Self-Organizing Linear Output	
SOM	Soil organic matter	(%)
SR	Solar radiation	(W m <sup>-2</sup> )
SWC	Soil water content	(m <sup>3</sup> m <sup>-3</sup> )
$T_{air}$	Air temperature	(°C)
TERN	Terrestrial Ecosystem Research Network	
TDR	Time-domain reflectometry	
$u^*$	Friction velocity	(m s <sup>-1</sup> )
VPD	Vapour pressure deficit	(kPa)
VWC	Volumetric water content	(mm)
$w$	Vertical wind velocity	
$WUE_i$	Intrinsic water-use-efficiency	(μmol mol <sup>-1</sup> )
eWUE	Ecosystem water-use-efficiency	(μmol mol <sup>-1</sup> )
$_{int}WUE$	Instantaneous water-use-efficiency	(μmol mol <sup>-1</sup> )
WW	Well-watered treatment	
WS	Water-stressed treatment	
<sup>13</sup> C	Carbon isotope with an atomic weight of 13	
<sup>12</sup> C	Carbon isotope with an atomic weight of 12	
$\alpha$	Fractionation during CO <sub>2</sub> diffusion through the stomata	(‰)
$\beta$	Fractionation associated with reactions by Rubisco	(‰)
$\beta$	A function for a scalar reduction of a process	(normalized from 0 to 1)
$c_p$	Heat capacity of moist air	
$q$	A parameter to describe the non-linearity of $\beta$	
$q'$	Mix concentration of CO <sub>2</sub> or H <sub>2</sub> O	(g m <sup>-3</sup> )
$\gamma$	Psychrometric coefficient	

$\Psi_{\text{md}}$	Midday foliar water potential	(MPa)
$\Psi_{\text{leaf}}$	Diurnal foliar water potential	(MPa)
$\Psi_{\text{pd}}$	Pre-dawn foliar water potential	(MPa)
$\lambda$	Marginal water cost of plant carbon gain	(mol H <sub>2</sub> O mol <sup>-1</sup> C)
$\Gamma^*$	CO <sub>2</sub> compensation point	
$\phi$	Quantum yield	( $\mu\text{mol CO}_2 \mu\text{mol photons}^{-1}$ )
$\Delta$	Stable isotope discrimination or $\Delta^{13}\text{C}$	(‰)
$\delta$	Delta-isotopic notation	(‰)
$\sigma$	Standard deviation	
$\delta^{13}\text{C}$	Ratio of <sup>13</sup> C to <sup>12</sup> C	(‰)
$\delta^{13}\text{C}_{\text{air}}$	Carbon isotope ratio of the air	(‰)
$\delta^{13}\text{C}_{\text{bulk-leaf}}$	Isotopic compositions of bulk-leaf tissue	(‰)
$\delta^{13}\text{C}_{\text{sugars}}$	Isotopic compositions of leaf soluble sugars	(‰)
$Q_A$	Difference between net radiation flux and ground heat flux	
$\rho_a$	Density of moist air	(g m <sup>-3</sup> )
$\chi^2$	Chi-square test for goodness of fit	

# *Abstract*

Semi-arid and arid ecosystems occupy 45 % of the Earth's land surface and approximately 40 % of the global population live in arid and semi-arid regions. Ecosystem productivity in these regions is constrained by water availability, which is in general erratic, spatially variable and confined to short periods during the wet season. Globally, semi-arid and arid ecosystems dominate the inter-annual variability of the global land carbon (C) sink. In particular, Australian semi-arid and arid regions were estimated to account for 60 % of the 2011 global land carbon sink anomaly (GLSA). Despite the importance of these Australian arid and semi-arid environments, mechanisms that explain variability in rates of C uptake (at regional- and global-scales) and trends are poorly understood, and these ecosystems remain little studied.

Australia is an extensive and flat continent, of which 70 % is arid or semi-arid land. Two biomes dominate the central semi-arid region: (1) Mulga woodland, dominated by species of the genus *Acacia* (shallow rooted N<sub>2</sub>-fixing trees, from the Mulga complex of species); and (2) open *Corymbia* savanna where the dominant cover is spinifex (a C4 grass) with widely spaced tall evergreen *Corymbia* trees. These two ecosystems are found within the Ti-Tree Basin, Northern Territory Australia, where two eddy covariance systems has been in operation for the past 4 and 7 years within a Mulga woodland and *Corymbia* savanna respectively. The main objective of this research was to investigate ecosystem functioning of the two semi-arid woodlands, in order to improve our understanding of the interaction of terrestrial semi-arid ecosystems with the atmosphere, through measurements of C and water fluxes at ecosystem- and leaf-scales. The overall hypothesis was that differences in ecosystem vegetation composition and structure would be significant factors explaining differences in C and water fluxes across two disparate ecosystems. To accomplish this general objective, C and water fluxes were evaluated at different temporal-scales (i.e., diurnal, seasonal, annual and inter-annual) and different spatial-scales (from plot- to leaf-scales) within a Mulga woodland and a *Corymbia* savanna. I employed three different approaches to evaluate C and water fluxes: i) eddy covariance data (at plot-scale); ii) a range of *in situ* eco-physiological investigations (at leaf-scale); and iii) glasshouse experimentation (at leaf- and whole-plant-scale).

In 2011 during the GLSA, the Mulga woodland captured 131 g C m<sup>-2</sup> y<sup>-1</sup> and total annual precipitation was 565 mm. The most recent hydrological year studied (August to July 2016-2017) had the largest annual rainfall recorded during my monitoring of ecosystem fluxes (713 mm) and net ecosystem production (NEP) was 217 gC m<sup>-2</sup> y<sup>-1</sup>. In contrast to the Mulga woodland, the open *Corymbia*-savanna was a C source across most years (2012 to 2016), with

NEP ranging between -14 and -190 gC m<sup>-2</sup> y<sup>-1</sup>, but was a C sink during 2016-2017 with NEP of 115 gC m<sup>-2</sup> y<sup>-1</sup>. As a result of continuous monitoring of C fluxes, precipitation thresholds at which the two semi-arid woodlands switched from C source to C sink were identified for the first time. The pivot-point for the Mulga woodland was 262 mm y<sup>-1</sup> and 506 mm y<sup>-1</sup> for the *Corymbia* savanna.

The two semi-arid woodlands experience the same climatic conditions; hence, I observed that different climatic drivers (i.e., temperature, vapour pressure, soil water content) exerted similar influences over C and water fluxes across seasons. Intra-annual variability in C and water fluxes was mostly attributed to differences in SWC across seasons. However, different eco-physiological behaviours of co-occurring species within the Mulga woodland and *Corymbia* savanna contributed to explain differences in C and water fluxes between them. Dominant species at the Mulga woodland are highly adapted to periods of low water availability. Thus Mulga species were very water-use-efficient (WUE: trade-off between C gain *per* water loss) compared to species at the *Corymbia* savanna. This was demonstrated when evaluating responses of the  $g_1$  parameter (as a proxy of intrinsic water-use-efficiency; WUE<sub>i</sub>) to water availability. The Mulga woodland (at ecosystem- and leaf-scale) demonstrated large capacity for water consumption in wet periods and the plasticity to become highly WUE when experiencing water scarcity. In contrast, dominant species at the *Corymbia* savanna had larger water use (i.e., large stomatal conductance, at ecosystem-scale large rates of evapotranspiration) thus, smaller WUE compared to species at the Mulga woodland. The C4 spinifex grass can be highly productive at the *Corymbia* savanna during wet periods and, it is likely that the biomass produced during 2010-2011 was the fuel for photo-degradation of leaf litter, particularly of spinifex leaves in subsequent years, and this can explain the large negative NEP observed at the *Corymbia* savanna for much of the study period.

One of the novel aspects of the present research was to evaluate how soil water content drives WUE using the theory of the optimal stomata behaviour through the  $g_1$  parameter (a normalized metric of intrinsic water-use efficiency:  $\gamma$ WUE) and compared  $g_1$  values estimated from three different methods (leaf gas exchange, carbon isotopes and eddy covariance fluxes). Here my result showed discrepancies among methods and seasons. Thus, Seasonal and annual variation in  $g_1$  derived from the three methods in this present study highlights the concern that the generic use of constant values of  $g_1$  to describe stomatal functioning is not reliable when parameterizing global climate models (Medlyn *et al.*, 2017; Wolz *et al.*, 2017).

My research at a leaf-scale highlighted the importance of species-specific attributes in driving C fluxes in semi-arid Australia. Integrating plant eco-physiological responses of dominant species is an essential step for improving our understanding of C flux rates within a

Mulga woodland and *Corymbia* savanna. Comparing semi-arid ecosystems contributes to our understanding of ecosystem functioning and mechanisms underlying variability in rates of C and water flux within different ecosystems, which bring us closer to understanding global variability in C cycling in terrestrial ecosystems. The research at a leaf-scale highlighted the importance of species-specific attributes of co-occurring species driving C fluxes in central Australia. Understanding functional processes (i.e., C assimilation, stomatal behaviours plant water status) and the vegetation responses across different plant species and ecosystems is crucial for improving our ability to predict global change. There is now an opportunity to evaluate the inclusion of *in situ* observations and account for variations of C and water fluxes when applying earth systems models and terrestrial vegetation C models at regional- and global-scales.